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Experimental burrow system: pathway patterns and building behaviour for the earthworm *Aporrectodea longa*

BY

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Synopsis: In experimental conditions, the patterns of earthworm burrow systems are analyzed. Burrows are characterized as "centred" or "connected". An ageing process for burrow systems is proposed.

Keywords: Burrow system, Earthworm, Pattern, Behaviour, *Aporrectodea longa*.

INTRODUCTION

When the natural burrow systems of earthworms were described (KRETZSCHMAR, 1982), very little was mentioned about the characteristic patterns of these systems. The main reason was the complexity of the systems observed which involved more than one unique species of burrowing earthworm. Also, at the time of observation, it was impossible to determine the age classes of the burrows. Furthermore, after having observed the burrows individually using a destructive method, some quantitative properties of the whole system were computed but no graphic representations of the burrow network were possible.

Different attempts to describe burrow system patterns can be found in the literature. Some observations have been made by filling the burrow system with latex or plaster and obtaining a casting of the system (JOYNER & HAMMON, 1961, GREEN & ASKEW, 1965). The very broken structure of the burrow systems we are dealing with does not permit an image of the complete system to be obtained in this way (this technique is dependent on the burrow system connectivity), except for the case of a

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single burrow which is found for particular monospecific populations such as *Lumbricus badensis* or *Lumbricus polyphemus* (LAMPARSKY & KOBEL-LAMPARSKY, 1987). In this latter case, the full description has been made by the authors and it is obvious that the pattern observed cannot be considered as a network.

Experimental attempts have been made, generally using thin "slides" of soil (2 or 3 cm thick: MARTIN, 1982, for example) maintained between two pieces of glass through which it was possible to observe the burrows dug by the earthworms. Some branching figures could be observed, although this was not the main aim of the author.

There is no doubt that experimental conditions do not permit natural-like patterns of burrow systems; this is due to the wall effect which leads to structures more similar to 2D patterns, while the natural systems are obviously 3D figures. Moreover, the structures of natural burrow systems result from the activity of several species during a long period of time with unknown ageing processes. Nevertheless, the understanding of burrow system patterns does not simply require a reproduction of plausible systems but also requires an explanation of the way by which the observed natural patterns are constructed. Then, burrow systems obtained in experimental conditions, if these conditions are chosen to be relevant to this aim, may provide informations about the initial mechanisms which generated the patterns observed in natural conditions.

I. — MATERIALS AND METHOD

The earthworms used were collected from the top soil of a permanent pasture near Dijon (France). The animals were kept by hand sorting, three days before they were placed in the experimental columns. The earthworms *Aporrectodea longa* were individually placed, immediately after capture, in a Petri dish ($\varnothing = 10$ cm, volume $= 250$ cm^3) into water-saturated soil. After 48 hours, it was assumed they had attained their maximum water content and they were introduced in the compacted soil columns.

The soil used in the compacted column preparation was taken from the top 20 cm of the same permanent pasture soil and was sieved immediately at its natural water content to give a fraction between 1 and 4 mm. The compacted soil columns were obtained following the method described in KRETZSCHMAR (1991).

At the beginning of this experiment, earthworms were weighed and placed on the top of each column. The columns were then placed in a permanent dark room, at 13°C. This experiment started on 87/04/27; the observations of burrows were made on 87/11/12.

The burrow systems, as usual in these conditions, were almost entirely along the walls. In order to describe them, the plastic wall was cut along the vertical axis and opened to free the outside surface of the soil column. Burrows were very easy to observe and their image was redrawn on a transparent sheet of paper placed around the column. The discussion which follows is based on these true images of external part of the system which represent at least 90% of the total system, except for column 16 where the internal burrows contribute 25,2% of the total length (for total lenght estimation, see KRETZSCHMAR, in press a). It has been checked that no external burrow has connections with another part of the external system through the soil column (there were no hidden connections). Because the burrow diameter is very small in regard to the burrow length and the size of the column, it may be assumed that the 2D representation of the external burrow system is free of geometrical deformations. In the following discussion, all comments on the "burrow" concern only this external system.

TAB. I. – **Water content and compressing range for the different studied column.**

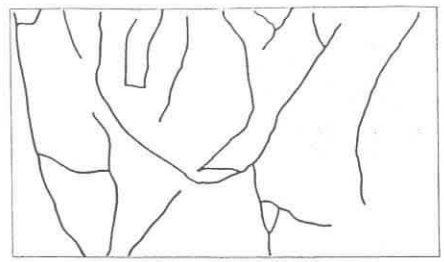
Compressing kPa \ Water content %	20	22.5	25
200	16, 17, 18		
275	13, 14, 15	10, 11, 12	
350	8, 9	4, 5, 6, 7	1, 2, 3

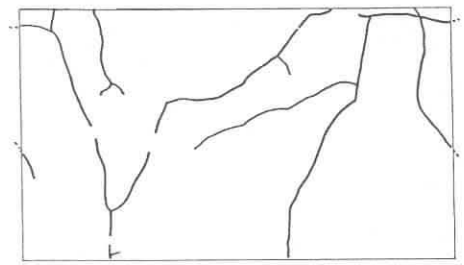
II. — RESULTS AND DISCUSSION

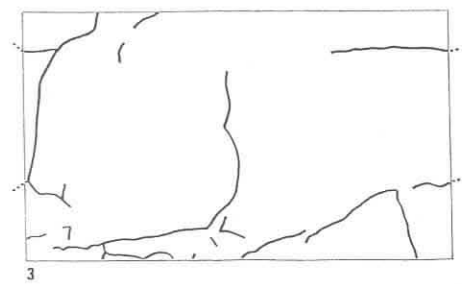
No relationships were found between the length of the system and or the weight of the earthworm which dug it, nor even the weight of cast production, porosity or bulk density (KRETZSCHMAR, 1991). The very rich variety of patterns which can be observed in such a situation (*figs.* 1 to 6) is due mainly to the individual variability and the complexity of behaviour determinism. Since we can consider the burrow system without any reference to the environmental conditions, an attempt is made to classify these different structures following their intrinsic patterns and following some assumptions on the behaviours involved in their creation.

Table II gives some quantitative elements for describing the burow systems. The difference between maximum (2060 mm) and minimum (542 mm) of the total length (Length) gives an indication of the variability of burrowing behaviour. The number of free extremities (Extrem) shows both the intensity of the branching and of the cutting up of the system while the number of nodes (Nodes) indicates the reticular aspect of the system. The correlation between Length and Extrem is greater ($r=0.83$, sign. 99%) than between Length and Nodes ($r=0.73$, sign. 99%), while the correlation between Extrem and Nodes is much less marked ($r=0.6$, sign. 90%). This could indicate that branching (Extrem) and reticular (Nodes) patterns are the result of two independent modes of behaviours. This is emphasized if Extrem and Nodes are first divided by the number of isolated units, whatever their size (in an isolated unit, the burrow is strictly continuous between any of the extremities of the unit; it may include several nodes and more than two extremities). Brk (Extrem/Units) and Ret (Nodes/Units) are closely correlated (0.94, sign. 99%). Hence, for one single unit, the number of extremities and the number of nodes vary in the same way while, at the scale of the entire system, these two parameters are quite independent, and are independent of the number of units, (i. e. independent of the size of the system). Two types of units can be therefore distinguished:

– the "centred" units where extremities are much more numerous than nodes: the simplest unit is a segment with 2 extremities and zero nodes; a more complex one is observed in the system 12 (*fig.* 4), back of the pictures, where 5 extremities and 2 nodes are counted;

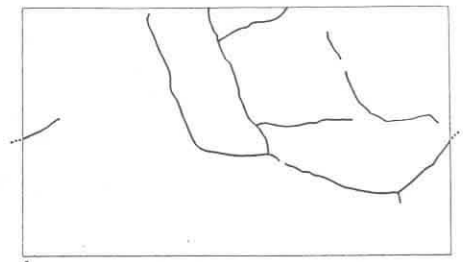


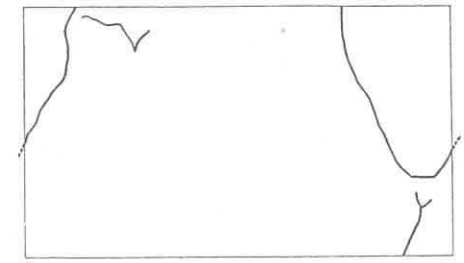


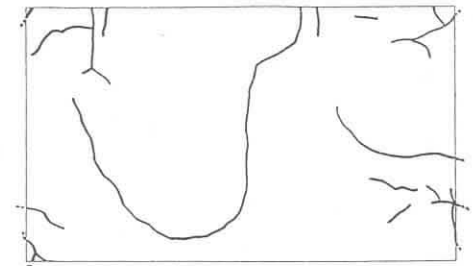


Legends of figures (dimension of the diagrams: 314 × 220 mm; burrows which are connected from the right of the left of the diagrams are marqued by dotted lines).

FIG. 1. – Patterns of peripheric burrow systems in the columns "25/350" (see table I).







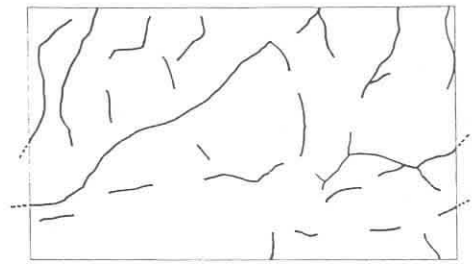


FIG. 2. – Patterns of peripheric burrow systems in the columns "22.5/350" (see table I).

TAB. II. – **Value of the pattern characteristics for the studied column (definition in text).**

N°	Length (mm)	Extrem.	Nodes	Units	Av. L. (mm)	Brk.	Ret.	S
1	1 745	25	10	8	218	3.12	1.25	0.4
2	1 162	19	8	6	194	3.16	1.33	0.42
3	1 176	28	5	11	107	2.54	0.45	0.18
4	727	12	4	4	181	3.00	1.00	0.33
5	542	7	1	3	181	2.33	0.33	0.14
6	1 049	28	7	10	105	2.8	0.7	0.25
7	1 432	46	5	21	68	2.19	0.24	0.11
8	585	10	2	4	146	2.5	0.5	0.2
9	1 623	50	18	17	95	2.94	1.06	0.36
10	1 571	53	4	25	63	2.12	0.16	0.075
11	1 046	18	4	6	174	3.0	0.67	0.22
12	636	16	6	6	106	2.67	1.0	0.38
13	1 332	18	7	7	190	2.57	1.0	0.39
14	802	17	3	7	115	2.42	0.43	0.18
15	2 060	30	27	3	76	10.0	9.0	0.9
16	791	19	1	9	88	2.11	0.11	0.053
17	814	5	1	2	407	2.5	0.5	0.2
18	1 506	29	6	11	137	2.64	0.55	0.21

– the "connected" units where the number on nodes is greater than the number of extremities; the best example is the large units of picture 15 (*fig.* 5), where 27 nodes and only 19 extremities are counted.

To compare the systems, it is useful to examine the ratio S = Nodes/Extrem which illustrates the intensity of the breaking of the systems. If this ratio is calculated on each segment, the influence of the small segment would be too important; therefore, this ratio is calculated for the entire system. To describe the systems completely, the density may also be used: Length is the most efficient index in this regard. From the value of S, the observed systems can be classified and some aspects of the building up and ageing phases of burrow systems can be proposed (the results discussed were obtained from burrow systems which were created over the same period of time); then when it is said that this pattern seems to be characteristic of a young or aged system, it is by reference to a hypothetical system. Some figures of this system are given by the animals in experimentation, which establish their burrows at different rates; the date of observation catches the different systems at different stages of development.

– $S < 0.2$: systems with mostly "segment" units. Following the density, two classes can be distinguished: low density on columns 5 (*fig.* 2), 8 (*fig.* 3), 14 (*fig.* 5), 16, 17 (*fig.* 6) and high density on columns 3 (*fig.* 1), 7 (*fig.* 2) and 10 (*fig.* 4). The first five systems could be considered as the first step in system development (system 5, *fig.* 1, is perhaps the best example) while the last three are rather achieved systems where the connectivity has been broken.

– $0.2 < S < 0.4$: systems appear to be young systems: 4, 6 (*fig.* 2), 11, 12 (*fig.* 4), 13 (*fig.* 5) and 18 (*fig.* 6) where attempts of reticulation are observable, which limits the type "centred" of these systems; in the case of system 9 (*fig.* 3),

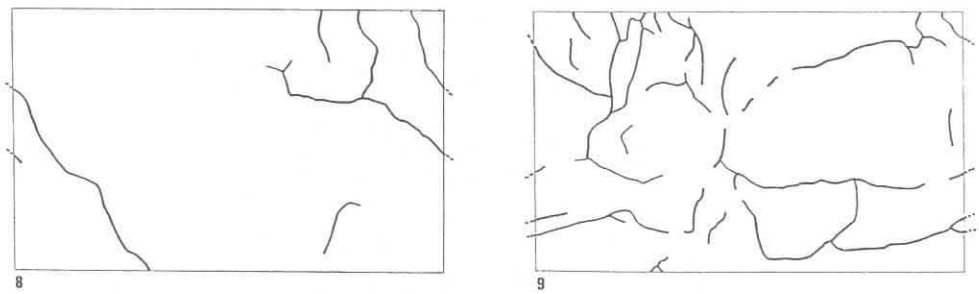


FIG. 3. – Patterns of peripheric burrow systems in the columns "20/350" (see table 1).

the breaking down of the system has been already begun, but connected units are still remaining.

– $S > 0.4$: these systems are characterized by connected units at different stages of development. It seems relevant to consider the pictures 2, 1 (*fig.* 1) and 15 (*fig.* 5) as a possible succession.

The different patterns, typical or combined or transformed by ageing of the systems, lead to a proposal of a mechanism for the settlement of the burrow systems. The first stage would be some "centred" burrow with very few nodes; the different segments could be initiated separately from the surface (example: 17 (*fig.* 6), 14 (*fig.* 5). Some connection would appear as in 11 (*fig.* 4) and 4 (*fig.* 2). The "connected" pattern would be developed to become similar to 15 (*fig.* 5); and finally the transformation of this quasi "tree-formed" system in a population of "centred" burrows, as in 10 (*fig.* 4).

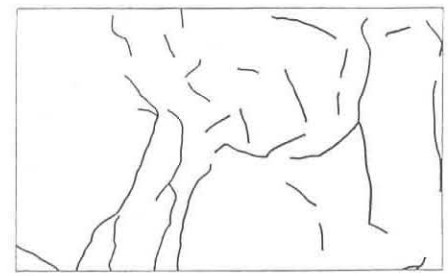
III. — CONCLUSIONS

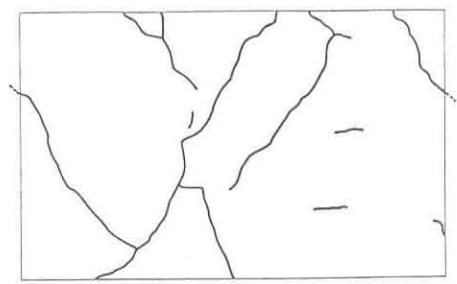
Despite some limitations in the experimental conditions, the observed burrow systems present coherent patterns which can be characterized. Two main transformations would occur regarding the natural systems:

– burrowing activity in this experimental situation is constrained by the size of the columns (what we can call the wall effect); this can leads to an increasing complexity of the pattern because earthworms move under spatial/physical stresses and not only under the spatial distribution of the biological factors on which they depend;

– over all, in this experiment, the observed systems result from isolated animals while, in natural conditions, the pattern of the system is related to the density of population and the variability of the behaviour among the numerous earthworms which may move through the same burrow.

In the studies of the stereological properties of simulated burrow systems (KRETZSCHMAR & MONESTIEZ, 1987; MONESTIEZ & KRETZSCHMAR, 1989), these two types of patterns, "centred" and "connected", have not been taken into account because they are rather difficult to observe in natural systems. However, they certainly exist much more frequently than has been thought previously.





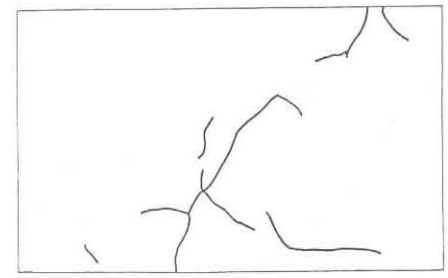
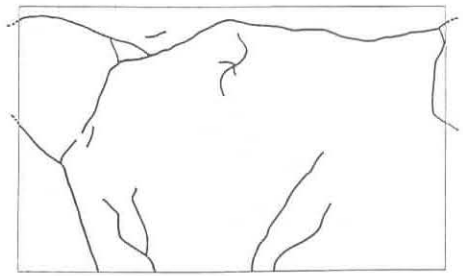
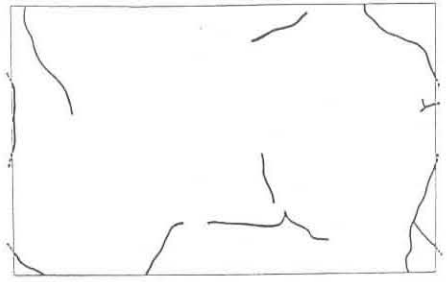


Fig. 4





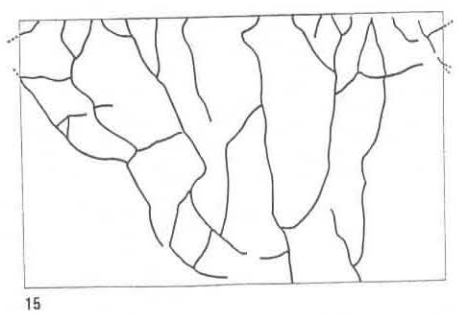
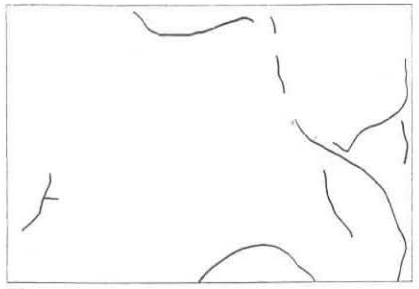
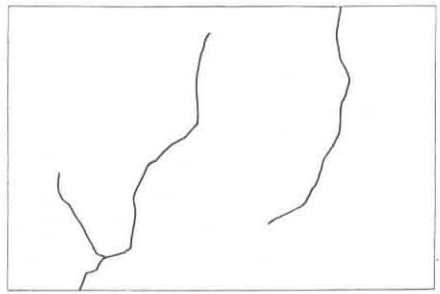


Fig. 5





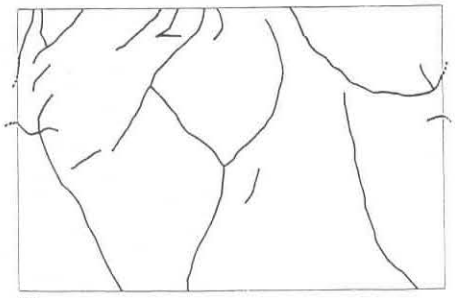


Fig. 6

FIG. 4. – Patterns of peripheric burrow systems in the columns "22.5/275" (see table I).
FIG. 5. – Patterns of peripheric burrow systems in the columns "20/275" (see table I).
FIG. 6. – Patterns of peripheric burrow systems in the columns "20/200" (see table I).

SUMMARY

Earthworms were introduced to soil columns (h = 30 cm; ∅ = 10 cm) composed of compacted seived aggregates. After 7 months of activity, the burrow systems in each column were described. The main part of the burrow system was along the column walls, and it was possible to observe different types of patterns.

Two main patterns are described: a "centred" pattern (which shows a diffusing activity from a central point) and a "connected" pattern where the number of nodes (connections between two or more burrows) leads to a network structure. The different patterns can be classified following an index of connectivity.

Despite the limitations of the experimental conditions, a relationship between the observed patterns and the earthworm behaviour can be inferred.

RÉSUMÉ

Système expérimental de galeries : types de structure et comportement constructeur du ver de terre *Aporrectodea longa*.

Des lombriciens de l'espèce *Aporrectedea longa* sont mis en élevage dans des colonnes de sols (h = 30 cm; ∅ = 10 cm) fabriquées à partir d'agrégats compactés. Après 7 mois d'activité, le système de galeries de chaque colonne est décrit. La majeure partie des galeries se trouve le long des parois. On y reconnait différents types de structures.

Deux structures essentielles sont décrites : un type « centré » (dans lequel les galeries diffusent à partir d'un point commun) et un type « connexe » dans lequel le nombre de « nœuds » (connexions entre deux ou plusieurs galeries) conduit à une structure en réseau. Les différentes structures sont classées suivant un indice lié au degré d'interconnection entre galeries.

Bien que cette étude soit faite en conditions expérimentales, on a pu identifier une relation entre l'évolution des structures des systèmes de galeries et le comportement d'*A. longa*.

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